

Phenology of the Sonoran desert-endemic populations of *Homalonychus selenopoides* (Araneae: Homalonychidae)

José Andrés Alvarado-Castro^{1,2} and María Luisa Jiménez¹: ¹Laboratorio de Aracnología y Entomología, Centro de Investigaciones Biológicas del Noroeste (CIBNOR), Av. Instituto Politécnico Nacional 195, Col. Playa Palo de Santa Rita, La Paz, B.C.S. 23096, México; ²Cuerpo Académico en Recursos Naturales, Universidad Estatal de Sonora (UES), Ley Federal del Trabajo y Perimetral s/n, Col. Apolo, Hermosillo, Sonora 83100, México. E-mail: a_alvaradoc@outlook.com

Abstract. *Homalonychus selenopoides* Marx, 1891 is endemic to the Sonoran Desert in Mexico and the southwestern United States. Despite its wide distribution in the desert, nothing is known about its phenology. For this study, we collected 464 immature and adult spiders and 67 egg sacs during late 2007 and throughout 2008. In the field, the life cycle is annual and phenology is markedly seasonal. Egg sacs and 2nd instar spiderlings occur in the field only from April–July, juveniles throughout the year, penultimate spiders from September–April, and adults of both sexes from November–April. Temperature and juvenile frequency were positively correlated ($r^2 = 0.9374$; $P < 0.0001$), but temperature and adult frequency were negatively correlated ($r^2 = -0.8904$; $P < 0.0001$). These spiders are active in winter and this is when the adults mature and mate. The phenology model proposed fits the winter-mature pattern of Aitchison (1984). Reproductive diapause governs the seasonal development of this species, which is possibly semelparous and univoltine.

Keywords: Homalonychids, seasonality, winter-mature, winter-active, reproductive diapause

In temperate zones, significant temporal changes occur in environmental conditions during the year. These seasonal changes in abiotic and biotic factors are periodic and predictable, and individuals of any population must adapt their life cycles to these changes (Roff 1992). Thus, periodicity of seasonally changing environments can synchronize the animals' developmental stages or activities to favorable times of the year (Schaefer 1977), or to help them escape from an unfavorable time in the same year (Krebs 1978). Spiders, similar to other arthropods, also coordinate their development with shifts in the environment using cues such as photoperiod, temperature, and availability or quality of food.

Phenology is the study of seasonal changes in population composition in relation to their environment (Jackson 1978). It helps us to understand how life history characteristics are shaped by natural selection. Although since the 1970s there has been increasing interest in the phenology of spiders (Jackson 1978), the life history and lifespan of few spider species have been investigated (Hallas 1989; Foelix 1996; Rybak 2007). The phenology of spiders has been documented in both field and laboratory studies, but phenology studies conducted in the lab poorly approximate natural conditions (Toft 1976). A comprehensive picture of the life history of a spider species in its natural habitat should include monitoring its activity throughout the year (Aitchison 1984).

Homalonychus selenopoides Marx, 1891 is a spider endemic to the arid regions of the North American southwest, including the desert plains of Sonora, México (Roth 1984; Crews & Hedin 2006). Recently, there has been great interest in determining different aspects of behavior (Domínguez & Jiménez 2005, Alvarado-Castro & Jiménez 2011), morphology (Duncan et al. 2007; Crews 2009), systematics, and phylogenetics (Crews & Hedin 2006; Miller et al. 2010) of homalonychid spiders, but there are still several aspects that are worthy of study.

The phylogenetic position of Homalonychidae remains elusive; a relationship with Lycosoidea (Domínguez & Jiménez 2005) and Zodariioidea (Miller et al. 2010) has been proposed,

among others. The morphological and biogeographical distinctiveness of these spiders suggest a long history of phylogenetic isolation (Crews & Hedin 2006). They use sand to powder their bodies, to build their eggsacs, and to build threads of silk and sand (Alvarado-Castro & Jiménez 2011). All of these features, besides the spiders' existence confined almost exclusively to the desert, make these spiders interesting subjects of study.

Here we describe the phenology of *H. selenopoides* in the field and provide hypotheses about its functional role in survivorship as well as the evolutionary significance of the natural history of these enigmatic spiders. We provide information about the strong seasonality of the different development stages; we also provide hypotheses about the relationship of these stages to the climate and biotic factors. Additionally, our results can be a solid basis for adequate planning of laboratory and field studies of this species.

METHODS

Study organism.—*Homalonychus* Marx, 1891 is a monotypic genus, the only representative of the Homalonychidae, and it includes only two species, *H. selenopoides* and *H. theologus* Chamberlin, 1924 (Roth 1984; Crews & Hedin 2006). The first species ranges in the Sonoran Desert from central Sonora northward to the Grand Canyon, including southwestern Arizona, southern Nevada, and southern California. A few populations have also been observed west of the Colorado River in the northern Mojave Desert. *Homalonychus theologus* ranges from the tip of the Baja California Peninsula northward to southwestern California and the southern end of Nevada (Roth 1984; Crews & Hedin 2006). We studied a population of *H. selenopoides* located at the southern tip of its distribution (Fig. 1). Aspects of taxonomy, distribution, morphology, habitat, and behavior of *Homalonychus* are summarized by Alvarado-Castro & Jiménez (2011).

Study area.—We collected spiders and egg sacs in the channel bed and sloping sides of the El Macapul arroyo and

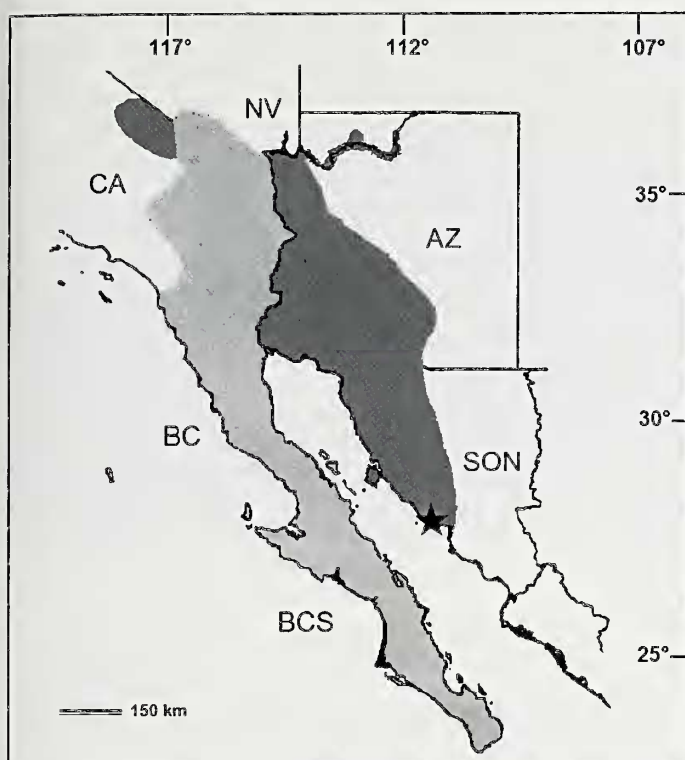


Figure 1.—Regional map, including distribution of *Homalonychus selenopoides* (dark gray) and *Homalonychus theologus* (light gray) (adapted from Crews & Hedin 2006). The collection area of *H. selenopoides* is also indicated (★). Abbreviations: SON, Sonora; BCS, Baja California Sur; BC, Baja California; AZ, Arizona; CA, California; NV, Nevada.

surrounding area (El Macapul) (27.9833° N, 111.0377° W and 28.02° N, 111.0508° W), including the entrance to Cañon de Nacapule, both north of San Carlos, Sonora, in the southern extreme of the Sierra El Aguaje. Climate, vegetation, and soil of the study area have been described in Alvarado-Castro & Jiménez (2011). We also collected some spiders inside the Cañon de Nacapule (Nacapule) (28.0155° N, 111.0541° W) and near Estero El Soldado (El Soldado) (27.9663° N, 110.9925° W) (Fig. 2).

We took weather information from CONAGUA station # 76256 (Observatorio “La Bola”), 23 km ESE from the study site, in Empalme, Sonora (27.9638° N, 110.8083° W). We used this information to construct a climate graph of the study region (1980–2008) (Fig. 3) for comparison with field data about phenology and to analyze the relationship between temperature and abundance of juveniles and adults.

Terminology.—We used the term “juvenile” to describe spiders from the 3rd instar to the antepenultimate stage prior to the maturing molt and the term “penultimate” to refer to the penultimate instar prior to the maturing molt. Because the mating and oviposition periods occur in different seasons in *H. selenopoides*, we refer to the reproductive season as when oviposition occurs (Schaefer 1977).

Determination of the developmental stage.—To verify the developmental stages of the spiders found in the field, we transported all of them to the laboratory at the Universidad Estatal de Sonora in Hermosillo, Sonora. Based on external morphology, we identified the following developmental stages

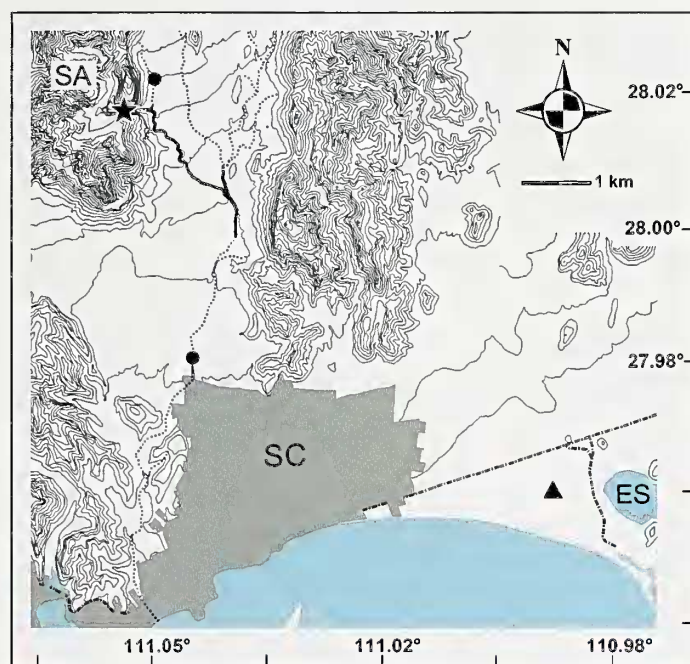


Figure 2.—Study area showing the collection sites of *Homalonychus selenopoides* specimens: Nacapule (★), El Soldado (▲) and El Macapul (section of arroyo highlighted with black). Two sites with unique collections are also indicated (●). Abbreviations: SC, San Carlos; SA, Sierra el Aguaje; ES, Estero el Soldado.

of the specimens: 2nd instar spiderlings, juveniles, penultimate spiders, and adults. The 2nd instar spiderlings were identified by their size; penultimate males were identified by the swollen pedipalp tarsi; and the penultimate females by the presence of epigynal lobes, which although poorly developed, were microscopically visible. Also, we identified the penultimate females easily when they matured after one molt in the lab. For this, the spiders were reared as described by Alvarado-Castro & Jiménez (2011).

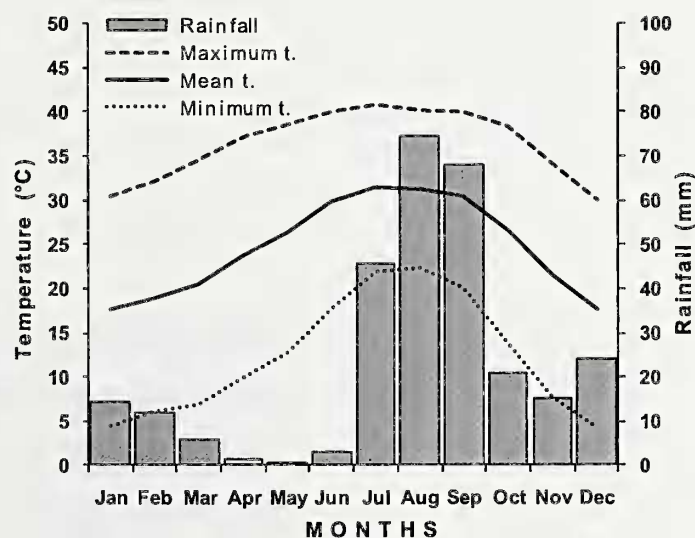


Figure 3.—Climate graph of the study region (“Empalme”, 29 years), including average rainfall and temperatures that occurred from 1980–2008.

Table 1.—Number of spiders and egg sacs of *Homalonychus selenopoides* found in each collection area by collection method. Percentages of spiders and total egg sacs are included in parentheses.

Collection areas	Hand collection		Pitfall trapping
	Spiders	Egg sacs	Spiders
El Macapul	437 (94%)	67 (100%)	14 (3%)
Nacapule	0 (0%)	0 (0%)	1 (< 1%)
El Soldado	9 (2%)	0 (0%)	3 (< 1%)

Phenology.—Field collection was conducted from November 2007–November 2008 to determine the frequency of each life stage of *H. selenopoides* throughout the year. We hand collected 3–5 days per month for a total of 43 collection days and also carried out pitfall trapping.

Pitfall trapping: We placed 10 pitfall traps each at El Macapul, Nacapule, and El Soldado. Each trap was constructed with one 2-liter plastic soda bottle, measuring 18 cm in height and 11 cm in diameter. The internal chamber contained ethylene glycol as the lethal agent. In each trapping month, we activated the traps for 14 days, and inactivated them the following 14 days.

Diurnal hand collections: Collections were made by 3–5 participants. We collected adult and immature spiders from under stones, dry cattle dung, wood, bricks, cardboard, or sheet metal; the egg sacs were found under rocks and dry cattle dung. We placed live spiders individually in plastic containers and transported them to our laboratory. Male and female voucher specimens were preserved in 75% ethanol and were deposited in the CIBNOR Arachnological and Entomological Collection (CARCIB) in La Paz, Baja California Sur, Mexico.

RESULTS

Collected spiders.—During our study we collected a total of 464 spiders and 67 egg sacs of *H. selenopoides* of which 451 spiders (97.2%) were at El Macapul and 13 spiders (2.8%) at the other collection sites (Table 1). Of these, in 13 months of pitfall trapping we caught only 18 *H. selenopoides*, which represented 3.9% of the total specimens we captured in the study area; most of these spiders were also caught at El Macapul (Table 1).

Phenology.—We collected 47 second instar spiderlings, 212 juveniles, 64 penultimate males, 22 penultimate females, 25 adult males, and 94 adult females. The presence and number of these stages of development changed during the year (Table 2).

The field life cycle of the population of *H. selenopoides* studied is annual. We found egg sacs from April–July with 21, 13, 27 and six egg sacs, respectively; most of them (91%) were

found during the months with lower rainfall (April–June) (Fig. 3). Egg sacs were usually found individually, although rarely we found two or three under the same shelter. All egg sacs were found hanging from the lower surface of the object (stone or cattle dung) that formed the ceiling of the shelter (Fig. 4). Second instar spiderlings were recorded from April–July. Juveniles were present almost all year round, but early juveniles were absent from December–January. Juveniles were scarce from November–April but were more numerous from May–October, reaching 100% of the collections in August. Penultimate spiders of both sexes were collected from September–April. Both sexes matured starting from November (Table 2). Females were present from November–May (only one female was collected in May), and males were present from November–April (Table 2), the cooler months of the year (Fig. 3). Juveniles comprised 100% of the collections from June–October with some 2nd instar spiderlings and penultimate instars at the beginning and end of this period, respectively (Table 2). The general phenology pattern is summarized in Fig. 5.

The relative abundance or the percentage of each developmental stage during the year had a partially overlapping unimodal distribution (Fig. 6), except for the penultimate stage, which had an irregular trend. Although outdated for a month, during the warmer months (March–November) the relative abundance of adults and abundance of penultimate spiders were positively correlated (linear regression, $r^2 = 0.9231$; $P < 0.0001$) whereas during the cooler months (December–February), no correlations were found. We found that the average temperature and the relative abundances of juveniles were positively correlated using a quadratic regression because of the high coefficient of regression ($r^2 = 0.9374$; $P < 0.0001$) whereas the average temperature and abundance of adults were negatively correlated using a linear regression ($r^2 = -0.8904$; $P < 0.0001$) (Fig. 7).

DISCUSSION

In this study, we provide relevant information about the basic ecology of *H. selenopoides*.

Pitfall trapping.—Even though pitfall traps have been the most widely employed sampling method for ground-dwelling arthropods, particularly cursorial spiders (Schmidt et al. 2006), we trapped only a few specimens of *H. selenopoides*. Thus, pitfall traps were useful only to confirm the mating period. We propose that mating occurs in winter, when we most often found both males and females. There is a consensus that the presence of adult spiders, particularly males, in pitfall traps

Table 2.—Number of *Homalonychus selenopoides* collected per month from November 2007 to November 2008, including their developmental stage and egg sacs. Numbers of egg sacs in italics are not added in totals per month.

Stage	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov
Egg sacs	0	0	0	0	0	21	13	27	6	0	0	0	0
2 nd Instar	0	0	0	0	0	10	17	16	4	0	0	0	0
Juveniles	4	5	0	5	6	10	17	33	27	40	34	19	12
Penultimate ♂♂	8	3	8	9	10	1	0	0	0	0	5	12	8
Penultimate ♀♀	0	1	3	2	7	1	0	0	0	0	1	6	1
Males	1	9	5	0	2	1	0	0	0	0	0	0	7
Females	7	11	27	21	8	12	1	0	0	0	0	0	7
Total/month	20	29	43	37	33	35	35	49	31	40	40	37	35



Figure 4.—Egg sac of *Homalonychus selenopoides* in the field, attached to the underside of a rock.

indicates the peak of copulation period (Toft 1976; Aitchison 1984).

Phenology.—The phenology of the studied population of *H. selenopoides* is markedly seasonal, correlated in part with large seasonal weather fluctuations of the study region. This has also been reported for some salticid spiders (Jackson 1978).

Crews & Hedin (2006) mention a time of development and longevity of *Homalonychus* females of up to five years in the lab. Although it is known that these traits are different in the field, we were surprised that the *H. selenopoides* life cycle in the field was annual, as in most species of spiders in temperate regions (Gertsch 1979; Foelix 1996). However, the majority of temperate-region spiders have spring-summer reproduction and overwinter as immatures (Kiss & Samu 2002; Rybak 2007). There are different proposed pattern types of life cycle or phenology (e.g., Toft 1976; Schaefer 1977; Aitchison 1984) based on duration of the life cycle, overwintering stage, seasonal peaks of activity, and reproductive period or seasonality of adults. During the winter collections, we did not observe dormancy in adults (or in penultimate spiders or juveniles). Because we infer that adults mate during winter, the phenology model proposed fits the Winter-mature pattern of Aitchison (1984) (“Winter-reif” of Tretzel 1954). Our model also partially

fits the type V phenology of Schaefer (1977) (Stenochronous, Winter-active species), but in *H. selenopoides* the true reproduction (oviposition) occurs exclusively in spring.

In temperate latitudes, winter-active spiders are uncommon and represent only 9% of all the spider species studied (Schaefer 1977). In turn, only 15% of the winter-active spiders correspond to the “Winter-mature” category, but the full life cycle is known in only a few species. Although these “winter mature” spiders also mate in winter (Toft 1976; Schaefer 1977; Aitchison 1984), this does not agree with our findings with *H. selenopoides* with respect to seasonality of the other life cycle stages (e.g., overwinter stage, oviposition period, spiderlings emergence) most likely because of severe weather conditions. A more relevant comparison would be with other winter-mature desert spiders of annual cycle, but we found no published accounts.

Our model coincides with the months of sporadic collection of juveniles, males, females, and egg sacs reported by Chamberlin (1924), Roth (1984), and Vetter & Cokendolpher (2000) for *H. selenopoides*. Our study is also corroborated by sporadic collections of this species made from 2012–2015, except that we found a few egg sacs in February 2012 and 2015, when the previous winters were relatively warm.

Although similarities with the phenology of *H. theologus* could be expected, we did not find them. Domínguez-Linares (2002) found *H. theologus* females in October and two peaks of early juveniles, one in December and another in May–July. Additionally, Roth (1984) also reported males and females of *H. theologus* collected in October. Differences in phenology between both species of *Homalonychus* are feasible because the areas where they were studied are at different latitudes with different subclimates (García 1973; INEGI 2002), which in turn have consequent effects on vegetation and predator/prey abundance, as well as different temperatures yielding different growth rates.

Although *H. selenopoides* females constructed some egg sacs sequentially in our laboratory, we assume that this species is semelparous in the field. If we consider that females are monandrous (Alvarado-Castro & Jiménez 2011), reassuming their sedentary lifestyle after pairing, and that we rarely found egg sacs and females in the same shelter, we speculate that most females construct only one egg sac in their lifetime in the field. The risk of complete batch loss of the egg sacs in *Homalonychus* may be very low because females construct the egg sacs inside the same

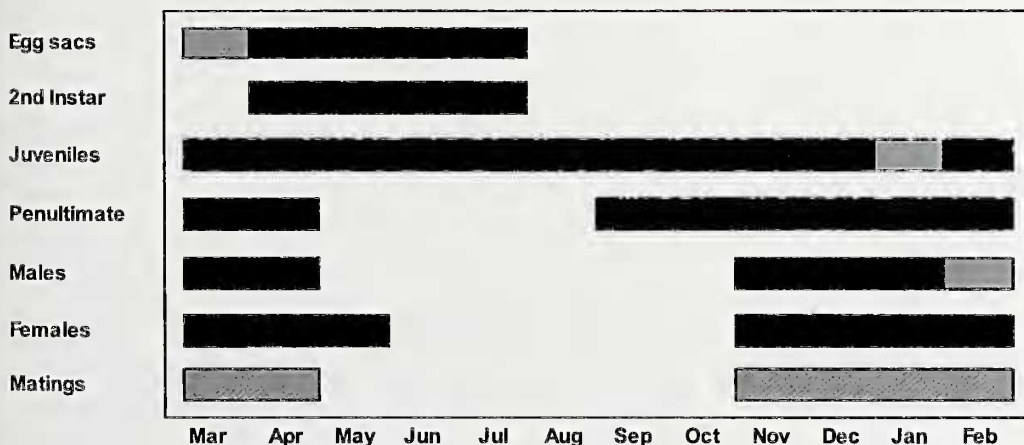


Figure 5.—Phenology model proposed for *Homalonychus selenopoides*. Hypothetical occurrence highlighted in gray.

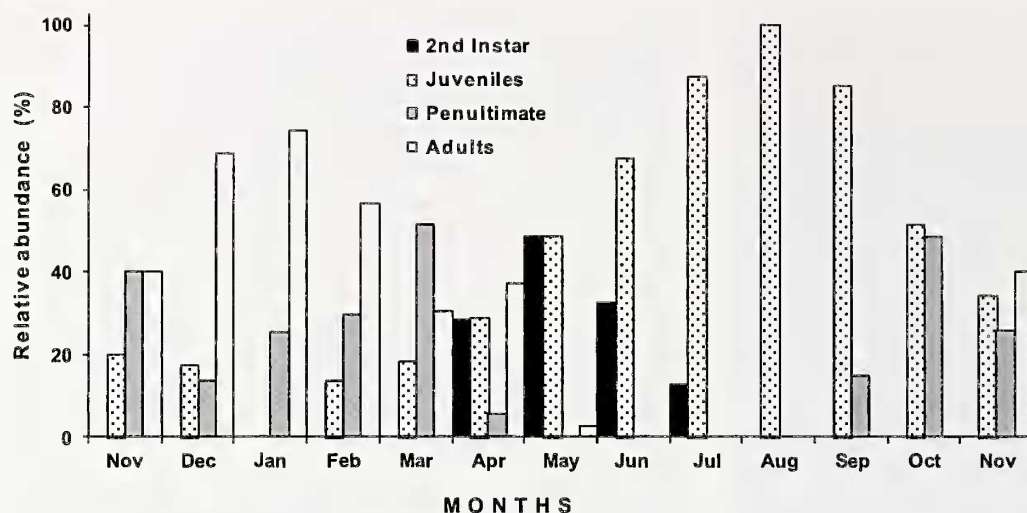


Figure 6.—Seasonal distribution of developmental stages of *Homalonychus selenopoides* during thirteen collection months. Relative abundance is the percentage of the total individuals collected per month.

refuges they occupy, and the elaborate structure of the egg sac provides significant protection of the eggs (Alvarado-Castro & Jiménez 2011). Thus, the conditions of the models of Murphy (1968) and Charnov & Schaffer (1973) that predict iteroparity do not seem to fit with *H. selenopoides*.

If *H. selenopoides* is semelparous, it is possible that it is univoltine like other desert spiders that have a single generation per year (Boulton & Polis 1999). Despite the potential for iteroparity and greater longevity, the one-year, one-egg sac pattern occurs in many desert arthropods due to the costly egg production and limited longevity in desert ecosystems (Polis 1991).

A season with lower temperatures is important in synchronizing the life cycles among individuals in the same population. In spiders, similar to insects, developmental cycles are controlled by photoperiod and temperature (Lees 1955; Schaefer 1977); also, these cycles can be partly defined by certain mechanisms of dormancy (Schaefer 1977). The photoperiod in our lab was natural, and the temperature, humidity, and

food availability were different between the laboratory and the field; however, the females started to construct their egg sacs simultaneously in both environments at the beginning of the spring. Thus, we infer that most likely the photoperiod controls the start of the oviposition period in *H. selenopoides*. Ultimately, changes in photoperiod are related to the evolution of physiological responses associated with diapause (Zimmermann & Spence 1998).

We propose that reproductive diapause (Schaefer 1977) of females governs the seasonal development of *H. selenopoides*. Diapause plays a central role for synchronizing the development of many univoltine arthropods (including spiders) with seasonally changing environments. Diplochronous spiders that mate in autumn and lay eggs in spring have reproductive diapauses. This is induced by short days, with inhibition of the development of the female reproductive system and the deposition of yolk. With long days, diapause is averted (facultative diapause) (Schaefer 1977).

We found egg sacs in the field only during spring and early summer. Some conjectures can explain this trait. Oviposition coincides with the start of insect abundance and increased temperatures that favor faster development of embryos and juvenile spiders. Moreover, these juveniles will have a long warm period (spring–autumn) to mature. Because laying eggs occurs only in the months of the lowest or no rainfall, we suggest that, additionally, this may be a strategy of ecological escape from the summer monsoon. Egg sacs may be vulnerable to surface water runoff because they are constructed with silk and sand at ground level (Alvarado-Castro & Jiménez 2011).

The absence of *H. selenopoides* males in the field from May is explained by their short lifespan. Males were less than one third as abundant as females in the field, which suggests their higher mortality, in line with the higher mortality rate of males reported by Rybak (2007) for *Bathypantes similinus* (now *B. eumensis* L. Koch, 1879) (Linyphiidae). Domínguez-Linares (2002) reported longevity in the laboratory of only 76 days for *H. theologus*. Because females began to mature in the field in November and they virtually disappear by May, we assumed that females had a catastrophic mortality during spring. Indeed, spring is the season with less precipitation in our study area. The cost of egg production reduces longevity of

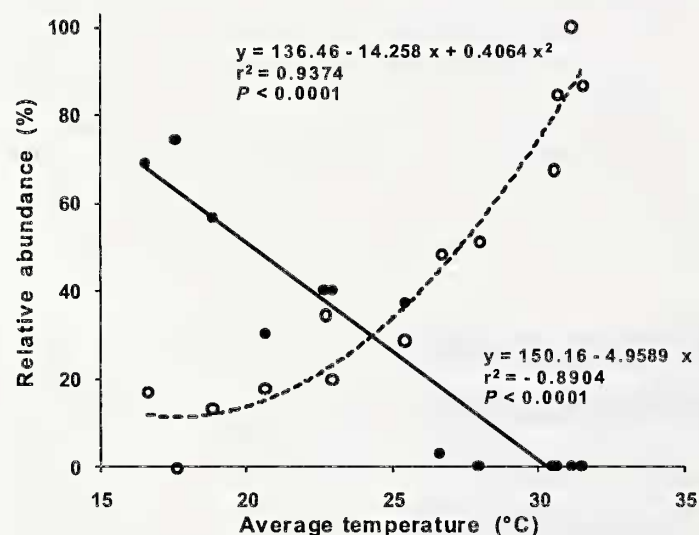


Figure 7.—Relationship between average temperatures and relative abundance of *Homalonychus selenopoides* juveniles (—○—) and adults (—●—) in the field.

arthropods in desert ecosystems (Polis & Yamashita 1991). In the desert spider *Diguetia mojavea* Gertsch, 1958 (Diguetidae), an inverse relationship was found between adult density and egg sac density, and females were not found after the oviposition period (Boulton & Polis 1999).

Adult activity in winter can be another strategy of ecological escape. In the field, many females had an enlarged opisthosoma and were clumsy to escape or did not flee. Thus, it seems reasonable that adult females that may be unable to avoid predators occur during winter when predators (i.e., other spiders, scorpions, solifugids, centipedes, and lizards [Cloudsley-Thompson 1983, 1995; Punzo 2003]) are hibernating or are less active (Muma 1974; Crawford et al. 1975; Polis 1979; Baltosser & Best 1990; Prentice 1997; Punzo 2003). This would explain the inverse relationship between the abundance of adults and the temperature, because the higher the temperature, the higher the predator activity. If this phenological feature reduces the possibility of an encounter with predators, then it is an adaptive anti-predator strategy of the primary type (Cloudsley-Thompson 1995). Other adaptive advantages of winter active or winter-mature spiders have been suggested by Jackson (1978) and Huhta & Viramo (1979).

Concluding remarks.—It would be useful to know the phenology of the most northern populations of *H. selenopoides* (e.g., those south of the Great Basin where the temperatures are colder in winter) to compare with our results. It would help to understand how climate shapes the phenology of this species, as well as how their populations respond to achieve inclusive fitness in different extreme environments. Additionally, a study of *H. theologus* life history strategies compared with that of *H. selenopoides* could be productive. It seems there are important differences in the phenology of both species, and our understanding of the evolution of these differences can likely be clarified by this kind of study.

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